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The Theoretical Significance of Vernalization

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THE THEORETICAL SIGNIFICANCE OF VERNALIZATION.

By

PROFESSOR N. A. MAXIMOV.

[Corresponding member of the Academy of Sciences in U.S.S.R.]

Institute of Grain Husbandry, Saratov, P.O. 20., U.S.S.R.

[Translated from Russian.]



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INTRODUCTION.

Since the publication of our Bulletin No. 9, prepared in collaboration with the Imperial Bureau of Plant Genetics, Cambridge, research on vernalization has been proceeding rapidly in U.S.S.R. ; laboratories and experiment Stations in all parts of the Union have approached the problem from a number of different aspects. An attempt is made to include abstracts of as many papers as possible in *Herbage Abstracts*, and reviews of the more important papers in *Herbage Reviews*.

Many statements for and against the theory and practice of vernalization have appeared in the scientific and popular agricultural literature, and it has been considered desirable to obtain from an eminent physiologist in the Soviet Union an authoritative account of the research which is now in progress in that country, with particular reference to the theoretical aspect. The Herbage Bureau has been most fortunate in obtaining the collaboration of Professor N. A. Maximov for this purpose and wishes to tender sincere thanks to the reviewer for the concise manner in which it has been done.

It should be noted that the next joint Aberystwyth-Cambridge Bulletin on the subject [*Herb. Rev.* 2. 83. 1934] is still in preparation. This opportunity is taken of asking all investigators who have not already advised either the Cambridge or Aberystwyth Bureau of the progress and results of their trials to favour one or other of these Bureaux with a brief statement along these lines. A wide international exchange of opinions and results on this most important subject through the medium of the Bureaux will thereby be facilitated.

R. O. WHYTE.

THE THEORETICAL SIGNIFICANCE OF VERNALIZATION.

One of the most significant achievements in plant physiology during recent years is undoubtedly the method of accelerating the development of agricultural plants as evolved by T. D. Lysenko at the Odessa Institute of Plant Breeding which has received a wide repute under the name of method of "*jarovizacii*." This Russian word has gradually been adopted in foreign literature, partly in some modified form, such as *yarovization* or *jarowization*, and partly in a latinized form, namely, *vernalization*. Such an adoption of a new term from a foreign language is undoubtedly one of the indications that here we have an entirely new conception which does not fit into the frame of usual terminology.

What is vernalization? Firstly, it is a practical agricultural method of accelerating the development of plants. As a result of vernalization, winter plants bear fruit in the first year, and late flowering plants become early flowering. At the same time, vernalization is one of the greatest achievements of that new trend of plant physiology which, not being satisfied only with the most detailed possible objective description and interpretation of phenomena occurring in living organisms, makes an effort actually to control these phenomena by subjecting their process to the active will of man.

As regards technique, the method of vernalization is extremely simple and easy. It is based essentially upon the fact that, by means of soaking, seed is transferred from a state of rest into a state of active life; at the same time, however, soaking is not continued until complete absorption of water, thus preventing growth from proceeding at full speed. Such partially soaked seed may for a fairly long time be retarded in growth at the initial stages of germination, when the tip of the root of the embryo has just penetrated through the seed coat. Such a retardation of growth makes it possible to subject the seeds to the required influences during a period of time sufficient for evoking in them those changes which will subsequently result in an acceleration of plant development.

In its most pronounced and first investigated form, namely, the "transformation" of winter plants into spring ones, or more precisely, the induction in them of an ability to ear in the first summer when sown in spring, the principal factor of vernalization is the influence of low temperature. Partially soaked and, therefore, slowly germinating seeds of winter plants are exposed to a temperature little above 0°C. during a period of 15-60 or more days (according to the variety), after which they acquire the properties of spring (*jarovye*) plants; hence is the term "*jarovizacija*." They can be sown in spring and will produce a yield within the same summer, frequently even earlier than spring varieties of the same plant sown simultaneously.

In other plants the factor of vernalization is not low temperature, but, on the contrary, increased temperature. Such are thermophilic plants, e.g., millet, soybean and cotton, the germinating seed of which must be exposed for several days to a temperature of 20-25°C., or even 25-30°C., after which they acquire the ability to pass rapidly to the stage of fruit bearing even in a cool climate under temperatures at which such transition in unvernallized plants would be retarded or even impossible. I shall not dwell upon the practical details of vernalization of individual plants for these have been discussed in sufficient detail in a paper by R. O. Whyte and P. S. Hudson²⁹. The extreme simplicity and yet high efficiency of this method has been demonstrated by the fact that during the current year, 1934, about one million hectares have been sown with vernalized seed in U.S.S.R., and yet reports of failure in carrying out vernalization are very rare even in localities most

remote from scientific centres. Owing to vernalization it was also possible to obtain maturity of many varieties of barley and oats within the Arctic circle, where so far the cultivation of cereals was regarded as entirely impossible (Razumov and Smirnova.²³) All these facts which illustrate the significance of this new method for agriculture are widely known at the present time; therefore, I shall not dwell upon them, but shall try to devote my attention mainly to throwing some light upon the theoretical aspect of this most interesting process.

Lysenko himself in one of his recent papers ¹⁵ briefly formulates his theoretical conceptions as follows:—

- (1) Growth and development are not identical phenomena.
- (2) The entire process of the development of an annual seed plant consists of individual steps or stages.
- (3) The stages always proceed in a strict sequence and a subsequent stage cannot set in until the preceding stage has been completed.
- (4) Different stages of development of the same plant require for their completion different external conditions.

We shall analyse each of these statements in some detail.

Lysenko places greatest stress on the fact that growth and development are not the same phenomena. Growth is an increase in the size of a plant without any profound qualitative changes in the growing parts. Even the embryo of a seed consists of a rootlet, stem and leaflets, which are in an embryonic stage. Although the germination of seed and further growth of the vegetative organs are connected with an increase in their number, branching of roots and stems and appearance of new leaves, they are, in Lysenko's terminology, growth and not development. Under development he understands the transition of a plant into a new stage, qualitatively differing from the preceding stage and bringing it nearer to the final phase of its life (at least as far as annual plants are concerned), namely, to fruit bearing. Even the most vigorous vegetative growth, for instance, unlimited tillering of winter cereals when sown in spring, may not be associated with their approach to earing, and theoretically we can imagine an annual plant which will persist indefinitely long at the stage of vegetative growth. On the contrary, in a slightly sprouting seed, which externally does not show any traces of growth, under an appropriate complex of external conditions, developmental processes may be in progress and will become manifest after the seed is sown in an environment favouring growth. Thus, for instance, swollen seeds of winter cereals exposed for a sufficiently long time to a temperature of about 0°C., undergo during that time such profound internal changes that plants grown from them are capable of rapid earing, even when sown late in the beginning of summer, and do not exhibit the sterile state and unlimited tillering typical for winter cereals under those conditions. We shall not dwell upon the questions as to whether a complete separation between growth and development is possible, or whether the processes of development (in Lysenko's terminology) may progress in entirely resting plants. The necessity of dealing in vernalization not only with seed that has been soaked, but also with seed that has begun to germinate, appears to indicate a certain interrelation between growth and development. This fact, however, by no means undervalues the significance of the fundamental postulate put forward by Lysenko, namely, the absence of a complete parallelism between these two processes. Although the idea of the difference between growth and development is not of itself entirely new, and though even Klebs in 1918 ¹⁰ expressed similar suggestions, yet the emphasis laid upon it by Lysenko undoubtedly introduces much greater clarity into this fundamental question of the whole physiology of plant development. The confusion between these two terms which is still frequent is absolutely inadmissible.

The second of Lysenko's postulates, that the entire process of development consists of individual stages, can become quite clear only in connection with the first statement regarding the difference between growth and development. In plant morphology and in phenology connected with it, and hence in agricultural meteorology and other sciences, different stages or phases of plant development are frequently described. In any instruction for recording phenological observations on the growth of cereals, we find indication of such "stages" as the appearance of shoots, tillering, stalk formation, shooting, earing, flowering, milk, wax and complete maturity, etc. For other plants other stages are indicated, such as the appearance of the first or second leaf, branching, budding, flower unfolding, etc. From Lysenko's point of view, all these "stages," or at least the majority of them, are actually only externally visible milestones in the process of growth. Some of them do not reflect that any qualitative changes are occurring in a plant, for instance, such "stages" as the first or second leaf, tillering, branching, etc. Others, however, are indirect and frequently belated reflections of those internal changes, for instance, such "stages" as stalk formation in grasses or budding of some other plants, which indicate that in the plant the processes preparatory to transition towards reproduction have been, or are about to be, completed. Actual "stages of development" may not be directly associated with any visible morphological changes, and profound internal changes occurring in the plant may be revealed only under definite conditions. Thus, for instance, vernalized seeds by their external aspect or even by their anatomocytological characters differ in no respect from unvernallized seeds, and only after sowing in the field does the process of their further development demonstrate the sharp difference existing between the two. One of the most important and extremely difficult problems of the theory of vernalization is to detect some internal biochemical characters which will indicate whether or not a plant has passed through a definite stage of development; we shall deal with this question later.

The third of Lysenko's postulates is the existence of a strict sequence in the progress of individual developmental stages. If any one stage for some reason (most frequently owing to the absence of the external conditions required) has not been completed, the stage subsequent to it cannot commence. Of all the stages of development distinguished by Lysenko so far only two have been thoroughly studied. One is that which may progress in a plant when the embryo has just begun growth, and which he calls the stage of vernalization.* The most important factor for the completion of this stage is a definite temperature; some plants require for this purpose a low temperature, in addition to adequate air and definite moisture, whereas other plants need higher temperature. The following stage, upon which a plant may enter only when the stage of vernalization has been completed, Lysenko calls *svetovaja* (the photo-stage). Some plants require light to complete the photo-stage (again in a definite combination with temperature, moisture and air); while other plants need darkness. Different varieties of one plant require different doses of these factors. Further stages of development have not yet been sufficiently studied. In one of his recent papers, Lysenko¹⁵ suggests that there are altogether five stages; so far, however, he has not yet indicated what these stages are. From his point of view the entire development of plants represents of itself a chain of consecutive processes, not a single link of which can be either omitted or transposed.

The fourth and last of Lysenko's postulates states that each of the consecutive stages of development requires for its completion a very definite set of external condi-

*As we see, the term "vernalization" has a twofold meaning. On the one hand, this is the name for a practical method of accelerating plant development, on the other, a definite stage of development. Lysenko himself notes the inconvenience of such an inconsistent terminology: however, he considers it premature to give any precise nomenclature of individual stages of development until they have been studied in greater detail.

tions, varying for different stages and for different plants. Thus, for instance, to pass through the stage of vernalization, winter wheat requires a temperature of 0-5-10°C., an adequate supply of oxygen and a sufficient degree of moisture in seed. Conditions of illumination therein are of no importance. For the same plant, however, continuous illumination and a temperature of about 15-25°C. are the optimal conditions for the completion of the photo-stage. If the period of daylight is shortened to 8-10 hours, this stage does not proceed and, although the plant has already been vernalized, it cannot proceed to reproduction; for an indefinitely long period it will exhibit only vegetative growth. Such a prolonged suspension at the vegetative stage of development was observed by Garner and Allard⁷ in their experiments on photoperiodism. In one of their recent publications they describe how, by shortening the day, they succeeded in preventing long-day plants, namely, *Sedum spectabile* and *Cassia marilandica*, from producing fruit for a period of nine years. It sufficed, however, to give these plants a long day in order to terminate their enforced flowerless condition.

In plants of a physiological type other than wheat, for instance, millet, the conditions for completing the stage of vernalization and photo-stage will be altogether different. Swollen seed of millet should be exposed during 5-7 days to a temperature of about 20-25°C. for vernalization, whereas the photo-stage progresses only under a shortened day and even better in complete darkness. Prolonged exposure in darkness of green plants which are already growing is, of course, impossible, for this may cause starvation and even death. But if the photo-stage will be induced, as is the stage of vernalization, at that time when the plants are as yet in the form of semi-swollen seed, the experiment may be carried out in complete darkness. In Lysenko's opinion, the whole essence of photoperiodism of short-day plants consists in that for the completion of the photo-stage they require an exposure to darkness during a definite number of hours. If this definite number of hours is given to them through an uninterrupted exposure to darkness, they pass rapidly through the photo-stage and then they can flower if cultivated under continuous illumination. If, on the other hand, they are subjected to an alternation of dark and light hours, the completion of this stage will be prolonged, whereas an excessively long day or continuous illumination make it altogether impossible for them to pass through this stage.

Completion of every stage of development signifies in itself, after Lysenko, a definite qualitative and irreversible change which has taken place in a plant. What these qualitative changes are, Lysenko has not been able to discover; he only refutes the interpretation repeatedly suggested from some quarters that here we are dealing with an accumulation in plants of specific hormones. Against the hormone theory he puts forward his own observation that the state of vernalization does not spread from one part of a plant to another. In this case we have the same strict localization which was observed by Garner and Allard in photoperiodism⁶. Recently one of the collaborators of Lysenko, M. A. Bassarskaja, has published an interesting investigation¹, the object of which was to detect the difference between vernalized and unvernallized seed by means of staining reactions. This investigation showed that when sections of vernalized embryos of wheat, barley and millet are treated first with ferric chloride (FeCl_3) and then with potassium ferro-cyanide [yellow salt ($\text{K}_4[\text{Fe}(\text{CN})_6]_3$)] the cells of the embryonic tissue acquire an intense blue colour owing to the formation of Prussian blue; in unvernallized embryos, the Prussian blue is not formed. In the author's opinion this difference in reactions indicates that during vernalization the oxidation-reduction potential and acidity of the medium are changed. Similar attempts in this direction were also undertaken at the Physiological Laboratory of the Academy of Sciences in U.S.S.R. (A. Richter, V. Rancan and M. Pekker²⁴), but the

existence of direct relationship between the completion of the stage of vernalization and these changes in colloido-chemical properties of embryonic cells still remains to be proved.

The fact that the colloidal properties of plant protoplasm are actually changed by vernalization is indicated by the observations recently made by some authors (Vasiljev, Kuperman, etc.) that the winterhardiness of winter plants is considerably reduced by vernalization and that these plants tend to show the characteristics of spring plants. It is by the transit into the vernalized state that Lysenko explains the fall in the winterhardiness of winter plants with the approach of spring. In this connection the ecological significance of the fact that the vernalization of winter plants requires a very long (up to two months) treatment with low temperatures of about 0°C. can be readily understood. The strong preservation of the winter state (*ozimostj* = hibernization) assists them to retain a greater resistance to the frost, at least during the first months of winter, when there is as yet little snow.

Lysenko regards the duration of the exposure to low temperature required for vernalization as an indication of the degree of hibernization of a plant. This duration varies from 15 to 60 days or more, and accordingly weak, medium and strong winter forms can be distinguished. Since spring forms can also be vernalized, a fact which indicates the presence of a certain degree of hibernization in them also, the difference between spring and winter forms proves to be quantitative and not qualitative. An intermediate position is taken by the so-called *dvoručki*, or dual-purpose plants (Cf. Wechselweizen of German authors) which can be sown equally well as winter or spring crops.

Such is the theoretically important basis of the method of vernalization which has acquired such significance in the agriculture of the Soviet Union. The elaboration of this theoretical basis at the present time is still far from being completed and Lysenko himself has several times subjected it to partial revision. A better knowledge of Lysenko's extremely interesting conceptions will be gained only after the publication of his treatise on the theoretical bases of vernalization which is in the course of preparation; then also a more detailed criticism of his views will be possible. Now, to make the significance of Lysenko's research clearer, we shall deal with the state of the problem of controlling the rate of plant development before the discovery of these new trends.

Although for the general public and even for scientific circles of agronomists, geneticists and plant breeders, who are not familiar with physiological research, the idea of the possibility of "transforming" winter plants into spring ones, or late plants into early, etc., was altogether unexpected, nevertheless we are bound in justice to state that even before Lysenko's research a considerable body of experimental data had been accumulated in this field.

First, we should mention the work of Klebs, the pioneer and founder of the subject of the physiology of plant development. Klebs was the first who definitely challenged the conceptions that the cycle of plant development is altogether constant, unchangeable and conditioned only by internal hereditary characters of the organism. In place of these prevailing conceptions, Klebs⁹ presented a number of brilliant studies, first on low and then on higher plants, and evolved his theory that the cycle of plant development may be changed arbitrarily through the interference of man. According to his theory, the reproduction of plants, as well as other life processes, are to a great extent subjected to external conditions. By changing these conditions we can also change the course of plant development, arbitrarily accelerating or retarding it. All the changes in external conditions act upon the process of reproduction not directly, but through the changes in the internal state of the plant. The greatest significance was ascribed by Klebs to the change in the balance between carbohydrates, on the one hand, and minerals, especially nitrogenous substances, on

the other. Every external influence stimulating an accumulation of carbohydrates, such as bright light, low temperature, inhibition of translocation, etc., in Klebs' opinion, stimulates the onset of fruit bearing. On the contrary, intensive mineral nutrition, and, to an even greater extent, the abundant intake of nitrogen, stimulate vegetative growth and retard flowering.

In his last study ¹⁰ on flower formation in *Sempervivum* published in 1918, not long before the premature death of this outstanding investigator, Klebs distinguished the following three phases in the process of transition from the vegetative growth to reproduction, namely: (1) acquiring the stage of readiness for flowering (die Entstehung des blühreifen Zustandes); (2) the formation of rudiments of flowers (die Bildung der Blütenanlagen); and (3) the development of flowering inflorescences. According to Klebs, each of these stages requires, for its completion, a definite set of external conditions. The first stage, i.e., the preparation for flowering, requires low temperature and intensive illumination, when the required accumulation of carbohydrates is formed. The second stage, i.e., the formation of budding, passes most successfully under continuous light; the intensity of illumination may be very low, only 3-4 metre-candles; the red rays of the spectrum are of special importance. Finally, the third stage, i.e., the development of inflorescence may progress also in darkness if the rudiments of the flowers have previously acquired sufficient size. Under light, however, stronger inflorescences will be formed; here again the light acts, in Klebs' opinion, as a source of carbohydrates, stimulating the transition of fruit bearing. It is only the second stage, i.e., budding, upon which the light has a specific formative influence which is not directly connected with the change in the ratio between carbohydrates and mineral substances. From the point of view of his theory on the influence of external factors through the change in ratio between nutritive substances, this direct influence of light is entirely inexplicable.

The division of the process of the transit to flowering into several stages, outlined by Klebs in his last research, as well as the further study of the direct formative (photoblastic) influence of light, did not find a response in the research of his followers. It was veiled by his fundamental theory on the importance of the ratio between carbohydrates and nitrogenous substances, which received an especially wide recognition among American investigators. A great rôle was played in this respect by the important paper by Kraus and Kraybill ¹¹ on the vegetation and reproduction of tomatoes, in which the importance of the ratio between carbohydrates and nitrogen (C/N) in plants was particularly stressed. This research gave rise to a new trend in the theory of plant reproduction which, however, I am unable here to discuss.

In the fairly wide literature, which more or less supports Klebs' conceptions, the investigation of the greatest interest from the present point of view is that of Gassner ⁸ concerning the origin of the differences existing between winter and spring cereals. This investigation is the first scientific attempt to shorten the vegetative period of winter cereals and to force them to ear in the first summer when sown in spring. Gassner effected this through a slow germination of seed at temperatures of about 0°C. According to his conceptions, winter cereals differ from spring ones in having a definite requirement of cold at early stages of their development. If this requirement of cold is met, and this is effected through the germination of seed of winter plants at temperatures of about 0°C., which stimulates the accumulation of carbohydrates, they acquire the ability to progress towards fruit bearing. Gassner's data received a further investigation in the researches by Maximov and Pojarkova ¹⁸ and Maximov and Krotkina ¹⁹. It was established in the latter study that many spring varieties are also able to accelerate their development under the influence of slow germination at low temperatures.

Complete vernalization, however, was not achieved in the research of either Gassner or Maximov and his collaborators. Under temperatures slightly higher

than 0°C ., growth of seeds of winter cereals still progresses so rapidly that they are unable to pass completely to the subsequent stage of development before they are sown in the field. Therefore, such seeds produce plants which are able to ear during the first year only if sown sufficiently early in spring, when natural cold will complete in them the process of vernalization. A complete and unfailing vernalization was first achieved by Lysenko, owing to the fact that he applied chilling to seeds which were partially soaked and were therefore unable to grow rapidly.

A practical solution of the problem of vernalization of winter cereals had almost been achieved by I. M. Tolmačev of Kiev ²⁷ in his research published in 1928 in the same volume of Proceedings of the U.S.S.R. Congress on Genetics in which the first relevant paper by Lysenko ⁴ in collaboration with Dolgušin was published. In order to retard the growth of seed of winter wheat, Tolmačev applied incomplete soaking. By keeping such seed during two months at a temperature of 0°C . he obtained plants which at the latest spring sowing produced ears in the first year. Working with sugar beet, Tolmačev observed that seed soaked and exposed to cold produced plants with a considerably increased percentage of flowering during the first year. On the other hand, plants of sugar beet kept from the autumn throughout the winter in a warm conservatory, with electric illumination, lost the ability to form flowering stalks and fruit in the next year. Repeating this method every year, Tolmačev was able to maintain beetroot plants at the stage of vegetative growth for four years. But whenever one of those perennial plants of beetroot was transferred in winter to a cold conservatory, it proceeded to produce abundant fruit in the following summer.

Tolmačev gives a peculiar theoretical interpretation to his experiments. According to his conceptions, for the earing of winter plants and the flowering of sugar beet, an active vital phase must be completed in their "stem plasm," a definite work must be done and a sufficient amount of products of disintegration must be accumulated. In spring plants, the "stem plasm" is ready for its function at the time of seed maturity. Those conditions which stimulate the accumulation and preservation of the products of disintegration, for instance, low temperature, also stimulate fruit bearing, and, on the contrary, the absence of the accumulation of the products of disintegration during the intensive growth under the influence of light and high temperatures depress stalk formation. Tolmačev's observations that low temperature (about 0°C .) has a great influence upon the transition of biennials into the stage of stalk formation and then flowering are not isolated. Retardation of flowering of sugar beet plants by keeping them in a hot conservatory was mentioned by Klebs. In this respect, extremely instructive are the trials by J. Miller of Cornell University ²⁰ and ²¹, who by an analagous method prevented cabbage from proceeding to the emergence of inflorescence and obtained up to six consecutive heads on one stem. Similar trials with celery were conducted by Thompson ²⁶. All these phenomena come very near to the vernalization of winter plants, especially since in some biennials, as reported by Gassner ⁸ and Maximov ¹⁷, it was possible to obtain flowering in the first year through prolonged chilling of seed at the stage of germination. Undoubtedly, the problems of vernalization of biennial and perennial plants deserves greater attention than has so far been devoted to it, and needs a systematic investigation similar to that which Lysenko has made on the vernalization of annual plants.

These are the main researches which may be mentioned as the predecessors to Lysenko's investigations. There is no need to discuss them in greater detail, for the general position of the question on the regulation of the vegetative period in plants was already outlined by me in 1929 in a paper published in *Biologisches Zentralblatt* ¹⁷. Comparing our actual material with the theoretical conceptions formulated in this paper with what we have at the present time, it is possible to see particularly clearly the great theoretical and practical significance of Lysenko's research.

The recognition of the great importance of his work does not mean, of course, unrestricted acceptance of his theoretical statements without reservation. Thus, for instance, the categorical statement by Lysenko that for the vernalization of winter plants there is an essential complex of factors which ought to include a temperature not higher than 5-10°C., and that until the plants have received this complex they are unable to proceed to reproduction, can hardly be reconciled with the observations of many authors (Lebedincev,¹²; Oleinikova,²²; McKinney and Sando,¹⁶; Vasiljev²⁸ etc.). These authors showed that under favourable light conditions, especially by shortening the day during the first week of growth of winter cereals it is possible to induce fruit bearing in the first year, dispensing altogether with low temperatures.

On the basis of similar observations, Čailahjan³ considers that Lysenko tends to exaggerate the significance of the temperature factor. Čailahjan also refutes the theory of stages, and speaks in his work about the vernalization of plants by light.

Numerous authors have also challenged Lysenko's statements as to the complete irreversibility of the process of vernalization. Tolmačev, according to Ljubimenko¹³, has observed that vernalized winter seedlings lose the ability to produce ears rapidly when placed under the influence of X-rays, and considers this as indicating the loss of their vernalized state. According to an observation (as yet unpublished) made by Lebedev of Saratov, vernalized seeds recover the former grade of hibernation when kept dry for a considerable time. The reversibility of vernalization and its gradual acquisition were indicated also by Zerling and Čepikova³⁰ in studies on the vernalization of red clover and some other herbage plants. After studying the external indicators of vernalization in seeds and particularly the morphological peculiarities of the first leaves of the seedlings, Sereiskii and Sluckaja²⁵ have also shown the "possibility that under a definite combination of factors a plant can lose those properties which have been acquired during vernalization."

In a recent extremely interesting and carefully considered paper devoted to the problem of the artificial regulation of the length of the vegetative period in plants, Ljubimenko¹³ supports the idea of the partial reversibility of the process of development in plants. In the opinion of this investigator, "two periods must be distinguished in the state of the embryonic cells of a plant, namely, unstable, when the development can be turned in one direction or another, and stable, when such a change cannot be made." This statement Ljubimenko illustrates with some examples of the reversibility of plant development under photoperiodism, and also with the above-mentioned data of Tolmačev.

Finally, in certain cases the conception that vernalization accelerates plant development has proved to be not altogether correct. Vasiljev²⁸ has observed that under definite conditions of light, unvernallized winter wheat (Kooperatorka) eared in 92-97 days after sowing, vernalized in 54 days. If, however, we add to these 54 days the 45 days which must be spent in the completion of the vernalizing process and during which the developmental processes in the seeds were in progress, we obtain 99 days, i.e., the same period of time as in the unvernallized plants. Similar computations could also be made for some spring plants in order to show that in many, though far from all, instances vernalization does not accelerate plant development, but merely transfers part of the time required for development to that period when the plant is still in the state of a slowly germinating seed. The advantage of vernalization in these cases consists only in shortening the period from sowing in the field to flowering, and thus it may be placed on the same footing as preliminary growing in hot-beds or greenhouses before the thaw or the onset of warm weather. This consideration should be taken into account more particularly in the evaluation of the results of vernalization of thermophilic short-day plants such as millet or maize. It is quite possible that in future several types of vernalization differing in principle will be distinguished.

All these doubts and contradictions will suffice to show that the theory of vernalization is as yet far from being completely formulated. It is possible that some of these contradictions will not be valid after further revision, but others will certainly prove to be justified and will make the introduction of a number of changes and corrections in Lysenko's theory absolutely necessary. A single investigator or even a group of investigators around him, are, of course, unable to solve all the most difficult problems of the physiology of development. Therefore, it appears to me to be exceptionally valuable that, through the initiative of the Imperial Bureaux of Plant Genetics at Aberystwyth and Cambridge, Lysenko's work, so far published only in Russian, has become available in sufficient detail to a wide circle of geneticists and plant breeders throughout the world. In this short article, devoted exclusively to the theoretical aspect of vernalization, I should like to direct to these problems the attention of wide circles of physiologists, before whom an extensive and fertile field of research is now being opened.

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